Site fidelity and homing ability in *Hyla labialis* (Anura, Hylidae)

Horst LÜDDECKE

Departamento de Ciencias Biológicas,
Universidad de los Andes, Santafé de Bogotá, A. A. 4976, Colombia

A Colombian highland population of *Hyla labialis* was studied for 73 consecutive weeks by applying a unique toe clip combination to each of 304 adult male and 181 adult female individuals captured and released in the field. The analysis of a recapture record of 74 % for males and 43 % for females revealed that frogs released at their capture site were reencountered almost exclusively there (98 % males, 89 % females), hence demonstrating site fidelity. The majority of frogs translocated to a release site at a distance of up to 200 metres returned to their original capture site (58 % males, 53 % females), hence demonstrating homing ability. The frogs' spatial behaviour varied in relation to the breeding cycle of the population. After translocation between two successive breeding seasons, most males as well as females homed. When translocated during the breeding season, relatively more males homed and relatively more females remained at the foreign release site. Almost 30 % of all translocated frogs remained at the foreign release site and about 15 % were found at a third site. The short-term reaction to translocation was stronger in males (53 % homed) than in females (31 % homed), but as time passed the discrepancies leveled off and a year later no statistically significant differences remained between male and female spatial behaviour.

INTRODUCTION

Short or long lasting site fidelity and homing ability have been reported for several species of anuran amphibians belonging to different families (review in SINSCH, 1992b). Site fidelity may be related to stationary behaviour of territorial or brood-caring individuals (McVEY et al., 1981; STEWART & RAND, 1992; VAN WIJNGAARDEN & VAN GOOL, 1994), but in many cases seasonal migratory long distance movements are involved, where each individual exhibits its site fidelity and homing ability through active round trips between two or more places (breeding site, estivation site, hibernation site), carried out in a repetitive manner according to the reproductive cycle of the population (HEUSSER, 1968; GLANDT, 1986; SINSCH, 1990).

Site fidelity and homing ability have also been demonstrated experimentally by displacing individual frogs from their capture site to a different place at a certain distance, where they were released and either followed in order to see where they were heading (OLDHAM, 1966; TRACY & DOLE, 1969; SINSCH, 1988) or marked with the expectation

of recapture near their original capture site (SINSCH, 1990; RITKE et al. 1991; PAPI, 1992).

Most of these studies on site fidelity and homing ability have been conducted in the temperate zones of Europe (HEUSSER, 1969; RYSER, 1989; SINSCH, 1992a) and North America (OLDHAM, 1966; DOLE, 1972). However, these faculties have also been revealed for some neotropical frog species (DIXON & STATON, 1976, McVEY et al., 1981; CRUMP, 1986; SINSCH, 1988; STEWART & RAND, 1992; VAN WIJNGAARDEN & VAN GOOL, 1994).

The purpose of the present study was to examine site fidelity and homing ability in the neotropical frog species *Hyla labialis*. In this paper I report the results of an experiment designed to survey the spatial behaviour of this high mountain frog and to analyse it in relation to gender and reproductive activity of the population.

MATERIAL AND METHODS

STUDY AREA

The field study was carried out in the Parque Nacional Natural Chingaza nature reserve at 3500 metres in the eastern chain of the Andes mountains near the Colombian capital Santafé de Bogotá. This páramo is open grassland interspersed with spongy moss cushions and rosette plants (VUILLEUMIER & MONASTERIO, 1986). The ground is bog-like in many parts. Higher vegetation is sparse and patchy, consisting of small-leafed shrubs and the characteristic tall frailejones (several species of the genus *Espeletia*, family Compositae). The climate at this high altitude is cold and humid. There is a strong daily but only a small yearly temperature cycle. Daytime air temperatures may rise to 22°C when it is sunny, but mostly stay below 12°C, due to the usually heavy cloud cover and frequent rains. Nightly frosts occur occasionally, particularly in the dry season (December to March). The precipitation pattern in Chingaza is unimodal, peaking in June with about 260 mm of a total yearly rainfall of 1900 mm (SARMIENTO, 1986).

Hyla labialis was studied in a valley that stretches and slopes gently in a north-south direction for about 700 metres, where six groups of shallow ponds 100-200 metres apart (identified by the letters C, I, V, B, P and L) offered suitable breeding sites for this species (fig. 1). *H. labialis* was the only frog species that used these ponds for egg deposition. The only other frog species present in the study area, *Colostethus subpunctatus*, *Eleuthero-dactylus bogotensis*, and *E. elegans*, deposit terrestrial eggs.

BREEDING BIOLOGY OF *HYLA LABIALIS*

These frogs (male mean SVL 51 mm, female mean SVL 63 mm) usually breed in permanent ponds. Amplexus occurs in the water, where calling males are approached by receptive females. Whereas males spend several months per year in or near the breeding pond, females enter the water mainly for oviposition, which usually takes one night.
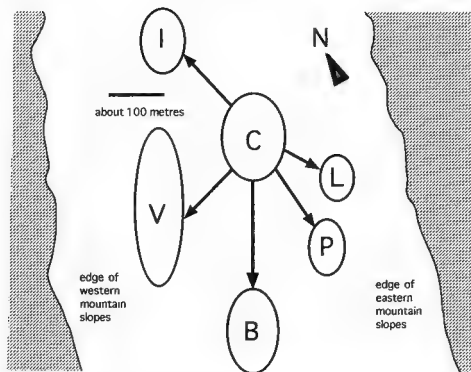
Fig 1. – Sketch of the mountain valley where the spatial behaviour of *Hyla labialis* was studied. Control frogs were captured and released in the central breeding area C. Experimental frogs from five breeding areas (I, V, B, P and L) were translocated to area C and released there. Arrows indicate the homeward directions and rough distances.

Females spend most of their life on land, up to hundreds of metres away from the water. Two main breeding seasons per year last from about one to three months each: one peaks in February-March, the other in September-October. Occasional breeding activity may occur any time, even during the driest months of the year, when there is little water in the ponds.

TESTING FOR SITE FIDELITY AND HOMING ABILITY

From June 1991 until August 1992, the six breeding areas were searched during daylight hours for adult *H. labialis* about once a week by slowly walking around the ponds in order to spot frogs visually. All encountered frogs were captured and censused. Many of these animals were already individually marked by toe-clipping from previous studies (LÜDDECKE, unpublished). All newly caught frogs were marked individually in the same manner. Most animals were released on the same day of capture, but some were kept in the laboratory for a week prior to their release. The search for marked frogs was continued until December 1992, but after August 1992 all encountered animals were released at their capture site.

To test for site fidelity, 187 frogs found in the central breeding area C were released at their capture site. To determine their homing ability, 298 individuals captured in the five breeding areas surrounding area C were translocated to area C and released there. Recapture of these translocated frogs at their original capture site would indicate homing behaviour.

STATISTICAL ANALYSES

Due to disparate amounts of data for males and females, and lack of normal distribution of data, many comparisons were made after converting actual counts into percentage numbers, or applying chi-square tests or non-parametric statistics (NEAVE & WORTHINGTON, 1988).

RESULTS

RECAPTURES

A total of 485 individual adult *Hyla labialis* were marked and released. Of these, 306 individuals were recaptured, yielding an overall recapture rate of 63.1 %. Recapture rates differed significantly between males and females (χ^2 = 45.6, P < 0.01). In both sexes, recapture rates were slightly higher for translocated frogs than for home-released frogs (Table 1). Recapture success was highest during peaks of breeding activity when frogs were abundant at the ponds. Time intervals between capture and first recapture ranged from one week to 73 weeks. The mean time interval between release and first recapture was shorter for males (18 weeks) than for females (23 weeks). During 26 weeks after initial release, the time span between two reproductive peaks, relatively more males (167 of 227, 74 %) than females (46 of 79, 58 %) were recaptured.

SITE FIDELITY

Of 86 individually marked males originally captured and released in the central breeding area C, 85 (98.8 %) were recaptured in the same area. The recapture rate for females (25 of 28, 89.3 %) at the original capture site was not significantly different from that of males (χ^2 = 3.22, P > 0.05). Four frogs left the home area and each moved to a different site.

HOMING ABILITY

Because there were no significant differences in homing between frogs from the five breeding areas surrounding C (χ^2 = 5.15, P > 0.05), I pooled the data from these areas

Table I. - Recapture record of individual adult male and female *Hyla labialis* handled in site fidelity and homing ability experiments in the Páramo de Chingaza.

Treatment	Males		Females	
	N	%	N	%
Released at capture site	86 of 119	72.3	28 of 68	41.2
Released after translocation to another site	141 of 185	76.2	51 of 113	45.1

Table II. - Long-term spacial behaviour of 141 adult male and 51 adult female *Hyla labialis* after translocation from their original capture site to a common central release site.

	Males		Females	
	N	%	N	%
Returned to original capture site	82	58.1	27	52.9
Remained at release site	42	29.8	14	27.4
Moved to third site	17	12.1	10	19.6

Table III. - Comparison of long-term spatial behaviour during and between breeding seasons of adult male and female *Hyla labialis* after capture and release in breeding area C and after translocation to C from all other breeding areas combined.

A. Breeding area C.

	During breeding seasons				Between breeding seasons			
	Males		Females		Males		Females	
	N	%	N	%	N	%	N	%
Site specific	46	98	17	89	38	97	8	89
Moved to another site	1	2	2	11	1	3	1	11

B. All other breeding areas combined.

	During breeding seasons				Between breeding seasons			
	Males		Females		Males		Females	
	N	%	N	%	N	%	N	%
Returned to capture site	35	55	16	52	47	61	11	55
Remained at release site	21	33	7	22	21	27	7	35
Moved to third site	8	12	8	26	9	12	2	10

(Table II). The majority of the frogs recaptured after translocation had returned to their original capture site. Some individuals homed within a single week, others were not seen again until more than a year later. Many translocated frogs were recaptured at the release site and others were found at a third site. The spatial behaviour of translocated frogs was significantly different from random (Goodness-of-fit test, $\chi^2 = 53.7$, $P < 0.001$). Both sexes showed the same general tendency and, in spite of some disparities, there was no significant difference between male and female spatial behaviour ($\chi^2 = 1.76$, $P > 0.05$).

SPATIAL BEHAVIOUR IN RELATION TO REPRODUCTIVE CYCLE

During the study period there were three reproductive peaks: October 1991, February 1992, and October 1992. The approximate length of each breeding season was determined by the presence of amplectant pairs and recently deposited egg clusters of *H. labialis* in the breeding ponds. Over the entire study period, males and females from the central breeding area C were equally site-specific, regardless of being released during or between breeding seasons (Table III).

To estimate the spatial behaviour of translocated frogs in relation to breeding activity, as a first approach I used first-recapture data covering the entire study period in order to look for long-term patterns (Table III). There were only slight and insignificant differences ($\chi^2 = 0.41$, $P > 0.05$) in male behaviour: a few less homed and a few more remained after translocation during a breeding season compared to translocation between breeding seasons. Females homed about equally well anytime and performed similarly to homing males. Considerably fewer females remained at the foreign release site and instead moved to a third site when translocated during the breeding season compared to their behaviour after translocation between breeding seasons. Due to this shift, there was a highly significant behavioural difference between females translocated during or between breeding seasons ($\chi^2 = 17.4$, $P < 0.01$).

In a second approach I used multiple-recapture data and set a time limit of ten weeks between release and recapture. This 10-week interval was presumably short enough to ensure that frogs had not yet entered their next reproductive phase. The males' short-term reaction was the same during and between breeding seasons. In contrast, female behaviour differed according to season: when translocated during a breeding season, more than half of the females remained at the foreign release site, but when translocated between breeding seasons, more than half of the females homed (fig. 2). Again, females behaved differently ($\chi^2 = 8.9$, $P < 0.01$) depending on the timing of translocation, but this time the shift occurred between returning and remaining frogs. Few males and females moved to a third site.
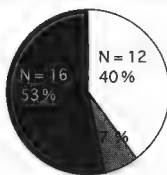
GRADUAL CHANGE IN SPATIAL BEHAVIOUR

Having found differences between the frogs' short- and long-term reactions to translocation, I examined how the spatial behaviour changed over time. I processed first-recapture data obtained from a sample of 110 individual frogs (86 males, 24 females)
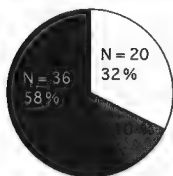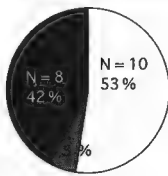
TRANSLOCATION BETWEEN BREEDING SEASONS
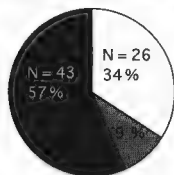
TRANSLOCATION DURING BREEDING SEASON

Fig. 2. — Spatial behaviour of male and female *Hyla labialis* within the first ten weeks after translocation either between or during breeding seasons, based on multiple recapture data. Black areas: frogs returned to capture site; grey areas: frogs moved to third site; white areas: frogs remained at release site.

captured during the same breeding season in the breeding areas surrounding C, translocated and released at C. When calculating the proportion of frogs in each behavioural category by accumulating data from sequential recapture-samples obtained first at the end of that breeding season (week 14), and afterwards at ten-week intervals, a gradual and statistically highly significant (Friedman Two-Way ANOVA, $\chi^2 = 11.07$, $P = 0.003$) change in the proportions of frogs in each behavioural category became evident as more and more frogs were recaptured (fig. 3).

Initially there was a large difference between the sexes: more than half of the males, but only one third of the females had homed. In contrast, proportionately more females
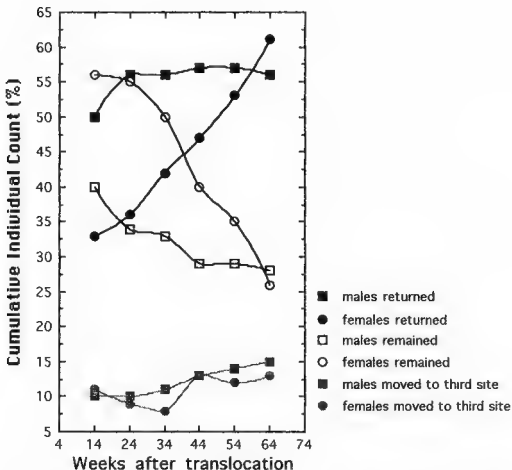
Fig 3 — Temporal change in spatial behaviour of 110 adult male and female *Hyla labialis* translocated in the same breeding season.

than males remained at the foreign release site during the first weeks after translocation. The relative numbers of males and females that moved to a third site were about equal. Almost six months later (week 24), males had attained a distribution approaching the final one, whereas that of females was still close to the initial one. However, when all individuals had been recaptured, the differences between males and females had almost vanished, and the situation resembled the long-term result for all translocated males and females (Table II) But the patterns of behavioural change over time differed significantly between sexes (match test $M_1 = 30$, $P < 0.05$).

DISCUSSION

RECAPTURE RECORD

Comparison of recapture rates reported for anuran species is difficult due to differences in capture schedule, search intensity and marking techniques, and conspicuousness, activity cycles and abundance of the species studied. With values over 70 % for males and over 40 % for females, the recapture rates for *Hyla labialis* were high compared with those reported for other anuran species (OLDHAM, 1966; HOTZ, 1970; RITKE et al. 1991; BUCHACHER, 1993). This may be related to my continuous capture-recapture programme over a period of 73 consecutive weeks, whereas most other studies relied on one capture period in the first year and a recapture period about one year later, both timed during breeding activity (OLDHAM, 1966; TRACY & DOLE, 1969; DOLE, 1972; RITKE et al. 1991; SINSCH, 1992a).

SITE FIDELITY

Male as well as female *H. labialis* showed a high degree of site fidelity, similar to the results obtained for *H. chrysoscelis* (RITKE et al., 1991), *Bufo americanus* (OLDHAM, 1966), and male *B. calamita* (SINSCH, 1992a). BUCHACHER (1993) obtained a lower site-fidelity rate of 67 % for *Pipa arrabali*, which he ascribed to a high mobility of individuals between adjacent ponds that were only a few metres apart. Remarkable cases of site specificity, where individuals were recaptured only a few metres distant from the original capture site, have been reported for male *Bufo bufo spinosus* in Italy (HOTZ, 1970), *Leptodactylus macrosternum* during the wet season in Venezuela (DIXON & STATON, 1976), and some territorial dendrobatid species (McVEY et al. 1981; VAN WIJNGAARDEN & VAN GOOL, 1994). This precision in site specificity was also observed in this study for some individual males and females of *H. labialis*.

The absence of site fidelity in *Bufo verrucosissimus* has been ascribed to the instability of suitable spawning sites in successive years (TARKHNISHVILI, 1994), and in *B. calamita* females to their opportunistic choice of the spawning site in response to calling males (SINSCH, 1992a). The strong site fidelity of *Hyla labialis* females conforms to the environmental conditions and reproductive biology of the population studied. Although long-term pond stability in the páramo is undocumented, the breeding ponds in the study area did not dry for several years, even during the strong El Niño year of 1992 (LÜDDECKE, personal observation). Thus site-specific females seem to run almost no risk in moving to a home pond and finding it dry. Because spawning may happen occasionally almost any month of the year, female *H. labialis* also benefit from being site-specific when the scarcity of males at the breeding ponds would offer little opportunity for long-distance phonotactic orientation to callers.

HOMING TENDENCY

Translocated adult *H. labialis* were recaptured at the breeding ponds mostly during the breeding season, indicating that frogs returned there for reproduction. The moderate percentage of homing *H. labialis* (56.8 %) probably was not due to increased mortality while moving across the terrain, since the recapture rates of translocated frogs were higher than those of home-site released frogs. If frogs recaptured at a third site are regarded as potentially homing, then about 70 % of the translocated individuals had this tendency. This interpretation seems justified by the fact that some translocated frogs detoured to a third site prior to returning to the home site. Another possible reason for the moderate homing success, in spite of the strong homing tendency, is related to the high site fidelity evidenced by the control group: a strongly site-specific individual (although it may migrate) could be familiar with just a small fraction of the entire valley that was used as the study area. This would mean that finding home after displacement was hampered in individuals whose release site lay outside their migratory corridor. Nothing is known about the orientation mechanisms used by *H. labialis*.

Almost 30 % of the translocated recaptured *H. labialis* remained at the foreign release site. One possible reason for this behaviour is that the release site (breeding area C) was an appropriate place for reproduction and was therefore accepted in exchange for the original site. Most remaining frogs were recaptured only once shortly after release and their long-term spatial behaviour is unknown. However, some frogs first recaptured at the release site were found at the original capture site on their second or third recapture, indicating that they had only delayed their homeward journey.

RITKE et al. (1991) pointed out that long intervals between release and recapture may be due to slow recovery from a reproductive effort. The sex difference in recapture rate of *H. labialis* translocated in one and recaptured in the next breeding season implies that about half of the females skipped every other breeding season and spawned only once per year, while most males participated in every breeding season. This would indicate that females recovered slower than males from a reproductive event.

Since shortly after translocation during the breeding season most females were still found at the release site (fig. 3), at first glance this would mean indifference as to where to oviposit. But it turned out that, when recaptured, most of these females had not yet spawned at the foreign release site. Half of the females found at a third site and most females that had already returned to their home site when recaptured shortly after translocation were still gravid (LÜDDECKE, unpublished data). These results are compatible with strong site fidelity and suggest that females have the tendency to oviposit at a familiar breeding site.

RESUMEN

Una población de *Hyla labialis* de alta montaña en Colombia fue estudiada durante 73 semanas consecutivas, aplicando un marcaje único a cada uno de 304 machos y

181 hembras adultos capturados y liberados en el campo. El análisis de los datos de recaptura del 74 % de machos y 43 % de hembras reveló que las ranas capturadas y liberadas en su sitio de captura fueron reencontradas casi exclusivamente allí (98 % de los machos, 89 % de las hembras), lo que demostró su fidelidad al hogar. La mayoría de las ranas traslocadas a un sitio de liberación a una distancia de hasta 200 metros regresó a su sitio de captura original (58 % de los machos, 53 % de las hembras), lo que demostró su capacidad de retornar al hogar. El comportamiento espacial de las ranas variaba acorde al ciclo reproductivo de la población: después de la translocación entre dos épocas reproductivas sucesivas, la mayoría de los machos y hembras retornaban al hogar. Después de una translocación durante una época reproductiva, relativamente más machos retornaban, pero relativamente más hembras se quedaban en el sitio de liberación. Casi el 30 % de las ranas translocadas se quedaba en el sitio de liberación y el 15 % fue encontrada en otro sitio distinto. La reacción inmediata a la translocación era más fuerte en los machos que en las hembras (53 % y 31 %, respectivamente, regresaban al sitio de captura), pero con el paso del tiempo las discrepancias en el comportamiento espacial disminuyeron y un año después no quedaron diferencias significativas entre machos y hembras.

ACKNOWLEDGEMENTS

LITERATURE CITED

BUCHACHER, C. O., 1993. − Field studies on the small Surinam toad, Pipa arrabali, near Manaus, Brazil. *Amphibia-Reptilia*, **14** 59-69

CRUMP, M. L., 1986. − Homing and site fidelity in a neotropical frog, *Atelopus varius* (Bufonidae). *Copeia*, **1986**· 438-444

DIXON, J. R. & STATON, M. A., 1976. − Some aspects of the biology of *Leptodactylus macrosternum* Miranda Ribeiro (Anura: Leptodactylidae) of the Venezuelan llanos. *Herpetologica*, **32**: 227-232.

DOLE, J. W., 1972. − Homing and orientation of the displaced toads, *Bufo americanus*, to their home sites. *Copeia*, **1972**: 151-158

GLANDT, D., 1986. − Die saisonalen Wanderungen der mitteleuropäischen Amphibien. *Bonn. zool. Beitr.*, **37**: 211-228

HEUSSER, H., 1968. − Die Lebensweise der Erdkröte (*Bufo bufo* L) Wanderungen und Sommerquartiere. *Rev. suisse Zool.*, **75**: 928-982.

----- 1969. − Die Lebensweise der Erdkröte (*Bufo bufo* L.): Das Orientierungsproblem. *Rev suisse Zool.*, **76**: 444-517.

HOTZ, H., 1970. − Zur Laichplatzökologie von *Bufo bufo spinosus* Daudin (Amphibia, Salientia) im tyrrhenischen Ligurien. *Vierteljahrschr. Naturforsch. Gesellsch. Zürich*, **115** 239-254.

McVEY, M. E., ZAHARY, R. G., PERRY, D. & MACDOUGAL, J., 1981. − Territoriality and homing behavior in the poison dart frog (*Dendrobates pumilio*). *Copeia*, **1981**. 1-8.

NEAVE, H. R. & WORTHINGTON, P. L., 1988. − *Distribution-free tests*. London, Unwin Hyman.

OLDHAM, R. S., 1966.   Spring movements in the American toad, *Bufo americanus. Can. J. Zool.*, **44** 63-100.

PAPI, F., 1992.   General aspects. *In*: F. PAPI (ed.), *Animal homing*, London, Chapman & Hall: 1-18.

RITKE, M. E., BABB, J. G. & RITKE, M. K., 1991. − Breeding-site specificity in the gray treefrog (*Hyla chrysoscelis*). *J. Herpet.*, **25**: 123-125.

RYSER, J., 1989. − The breeding migration and mating system of a Swiss population of the common frog *Rana temporaria. Amphibia-Reptilia*, **10**. 13-22.

SARMIENTO, G., 1986. − Ecological features of climate in high tropical mountains. *In*: F. VUILLEUMIER & M. MONASTERIO (eds.), *High altitude tropical biogeography*, Oxford Univ. Press.

SINSCH, U., 1988. − El sapo andino *Bufo spinulosus* análisis preliminar de su orientación hacia sus lugares de reproducción. *Boletín de Lima*, **57**: 83-91.

----- 1990.   Migration and orientation in anuran amphibians. *Ethol. Ecol Evol.*, **2**: 65-79.

----- 1992a. − Sex-biassed site fidelity and orientation behaviour in reproductive natterjack toads (*Bufo calamita*). *Ethol. Ecol. Evol.*, **4** 15-32.

----- 1992b. − Amphibians. *In*: F. PAPI (ed.), *Animal homing*, London, Chapman & Hall: 213-233.

STEWART, M. M. & RAND, A. S., 1992.   Diel variation in the use of aggressive calls by the frog *Eleutherodactylus coqui. Herpetologica*, **48** 49-56

TARKHNISHVILI, D. N., 1994. − Breeding of the toad *Bufo verrucosissimus*: sexual dimorphism and shifting spawning sites. *Amphibia-Reptilia*, **15**: 191-198.

TRACY, C. R. & DOLE, J. W., 1969. − Orientation of displaced toads, *Bufo boreas*, to their breeding sites. *Copeia*, **1969**: 693-700.

VAN WIJNGAARDEN, R. & VAN GOOL, S., 1994. − Site fidelity and territoriality in the dendrobatid frog *Dendrobates granuliferus. Amphibia-Reptilia*, **15**: 171-182.

VUILLEUMIER, F. & MONASTERIO, M. (eds.), 1986.   *High altitude tropical biogeography*. Oxford Univ. Press.

Corresponding editor: Janalee P. CALDWELL.